
A Synopsis of *Arabidopsis* (Brassicaceae)

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ABSTRACT. New combinations in *Arabidopsis* are proposed. Species previously placed in *Cardaminopsis* are here transferred to *Arabidopsis* and taxa previously recognized in *Arabidopsis*, other than *A. thaliana* and *A. suecica*, are excluded from the genus. Distributions and a key to the nine species and five subspecies are presented.

Based on analyses of rDNA sequences, the genus *Arabidopsis* as understood prior to this study is not only highly paraphyletic but also includes taxa that are distant in the Brassicaceae (unpublished results). This situation is particularly alarming given the central place that *A. thaliana* (L.) Heynhold plays in a myriad of current studies of genome evolution, developmental genetics, morphological evolution and development, etc. (Meyerowitz & Pruitt, 1985; Endress, 1992; Maluszynska & Heslop-Harrison, 1993; Crone & Lord, 1994; Larkin et al., 1994; Price et al., 1994; Teutonico & Osborn, 1994; Zhang & Lechowica, 1994; Tsukaya, 1995). Without a well-documented phylogenetic reconstruction of the genus and a congruent taxonomy, studies that make assumptions about its relations are likely to be inconclusive and to arrive at irrelevant conclusions. A number of recent studies (e.g., Maluszynska & Heslop-Harrison, 1993; Kamm et al., 1995; Tsukaya et al., 1997) have assumed close relationships between *A. thaliana* and species currently included in the genus that molecular data do not support (Price et al., 1994; O'Kane et al., 1995). The genus has been variously placed close to several other genera (*Arabis*, *Braya*, *Cardaminopsis*, *Cymatocarpus*, *Drabopsis*, *Halimolobos*, *Hylandra*, *Microsisymbrium*, *Nasturtiopsis*, and *Neotorularia*) based on morphological similarity (Hedge, 1968; Jafri, 1973; Al-Shehbaz, 1988; Ball, 1993). Rather than showing a close relationship among these genera, our work indicates that the circumscription of some of these genera and *Arabidopsis* is needed to better represent phylogenetic relationships. Recently, for instance, *A. erysimoides* has been moved to *Erysimum* (Al-Shehbaz, 1994),

A. parvula (Schrenk) O. E. Schulz has been transferred to *Thellungiella* (Al-Shehbaz & O'Kane, 1995), and both *A. gamosepala* Hedge and *A. tue-murnica* Kuan & An have been placed in *Neotorularia* (Al-Shehbaz & O'Kane, 1997).

The nomenclatural changes proposed here aim to align the taxonomy of *Arabidopsis* with the results of recent analyses of rDNA sequences (O'Kane et al., 1997) and on-going phylogenetic analyses. The changes given here were anticipated by both Hylander (1957) and Ball (1993). Hylander (1957: 602–603) stated that should *Cardaminopsis* and *Arabidopsis* be combined, *Cardaminopsis* “must be dropped into the latter genus [*Arabidopsis*], the limits of which would thereby be considerably widened—or, perhaps more correctly, drawn in quite another way than e.g. by Schulz.” Ball (1993: 322) echoed this by stating, “It seems probable that *Cardaminopsis* should be combined with *Arabidopsis*, and some species of *Arabidopsis* may have to be removed from the enlarged genus.” Furthermore, Jones (1964) suggested that *Arabis cebennensis* and *A. pedemontana* might better be placed in the genus *Cardaminopsis* (here *Arabidopsis*). These earlier morphological predictions are now strongly supported by two independent molecular studies: Price et al. (1994) using chloroplast DNA restriction site variation and *rbcL* gene sequences, and O'Kane et al. (1997 and unpublished) using nuclear rDNA sequences. Essentially, the nomenclatural changes proposed herein deal with the transfer of species from *Cardaminopsis* to *Arabidopsis*. Except for the nine species and five subspecies treated in this paper, all of the remaining 49 binomials variously assigned to *Arabidopsis* are excluded from the genus. Work is in progress to assign those to other genera.

Arabidopsis (DC.) Heynhold, in Holl & Heynhold, Fl. Sachsen 1: 538. 1842; nom. cons. TYPE: *Arabidopsis thaliana* (L.) Heynhold.

Cardaminopsis (C. A. Meyer) Hayek, Fl. Steiermark 1: 477. 1908. Syn. nov. Basionym: *Arabis* sect. *Carda-*

minopsis C. A. Meyer, in Ledebour, Fl. Altaic. 3: 19. 1831. Type not designated.
Hylandra Å. Löve, Svensk Bot. Tidskr. 55: 211. 1961.
TYPE: *Hylandra suecica* (Fries) Å. Löve.

The genus *Arabidopsis* can be recognized by the presence of short petiolate but never auriculate or amplexicaul cauline leaves, an indumentum of simple trichomes mixed with few-forked but never stellate ones, usually well-defined basal rosettes, white to lavender or rarely purple but never yellow flowers, erect to slightly ascending non-saccate or rare-

ly slightly saccate inner sepals, at least slightly to-
rulose, glabrous, compressed or rarely subterete to
terete fruits with a distinct midvein from base to
apex, uniseriate, wingless or rarely winged seeds,
and accumbent or rarely incumbent cotyledons.
The fact that *A. suecica* is an amphidiploid derived
from *A. thaliana* and *A. arenosa* (as *Cardaminopsis*
in most floras) (Hylander, 1957; Měsíček, 1967;
Suominen, 1994; Mummenhoff & Hurka, 1995;
O’Kane et al., 1997) further substantiates merging
Cardaminopsis with *Arabidopsis*.

KEY TO THE SPECIES AND SUBSPECIES OF *ARABIDOPSIS*

- 1a. Fruit terete; petals 2–3.5(–4) mm long; seeds usually plump; cotyledons incumbent *A. thaliana*
- 1b. Fruit strongly flattened, rarely subterete (*A. suecica*); petals (4–)5–10 mm long; seeds usually flattened; cotyledons accumbent, rarely obliquely incumbent (*A. suecica*).
 - 2a. Stoloniferous perennials; basal leaves orbicular or pinnate with (sub)orbicular terminal lobes [*A. halleri*].
 - 3a. Basal leaves entire or pinnate with weakly developed lateral lobes; lower cauline leaves orbicular to ovate, entire or crenate; flowering stems few, sparsely branched above . . . *A. halleri* subsp. *ovirensis*
 - 3b. Basal leaves pinnately lobed; lower cauline leaves oblong and dentate; flowering stems numerous, branched at base and often also above.
 - 4a. Basal leaves pinnatifid, with 1–7 lateral lobes; petals white to lilac; plants of Europe *A. halleri* subsp. *halleri*
 - 4b. Basal leaves lyrate; petals white; plants of Russian Far East, northeastern China, Korea, and Japan *A. halleri* subsp. *gemmaefera*
 - 2b. Non-stoloniferous perennials with or without branched caudices, or plants annual; basal leaves lanceolate, spatulate, oblanceolate, obovate, or rarely suborbicular, without orbicular terminal lobes.
 - 5a. Lower and middle cauline leaves distinctly petiolate, suborbicular to ovate, nearly as long as wide, dentate with few large teeth.
 - 6a. Petals 7–10 mm long, violet or sometimes white; plants 40–80 cm tall, sparsely pubescent; basal leaves acute at apex, longer than wide *A. cebennensis*
 - 6b. Petals 6–7 mm long, white; plants 15–30 cm tall, plants usually glabrous; basal leaves obtuse at apex, ± as long as wide *A. pedemontana*
 - 5b. Lower and middle cauline leaves subsessile or attenuate to a narrow base, much longer than broad, entire to small dentate, or lyrate to pinnatifid.
 - 7a. Cauline and basal leaves similar in shape and size (rarely cauline larger than basal) *A. croatica*
 - 7b. Cauline and basal leaves dissimilar in shape and size, basal leaves always larger.
 - 8a. Stems glabrous or rarely subglabrous; fruits horizontally spreading to slightly reflexed; petals becoming deep lilac; alpine areas in the Carpathian Mountains (Czech Republic, Slovakia, Romania, Poland, and adjacent Ukraine) *A. neglecta*
 - 8b. Stems sparsely to densely hairy at least below; fruits erect-ascending to subdivaricate; petals white or rarely pale lilac; sea level to various altitudes in Eurasia and North America.
 - 9a. Fruits weakly compressed to subterete; petals white, 4–5 mm long; cotyledons obliquely incumbent *A. suecica*
 - 9b. Fruits strongly compressed; petals white to lilac, (5–)6–8 mm long; cotyledons accumbent.
 - 10a. Petals with two small lateral teeth on the claw; basal leaves pinnatisect to pinnatifid [*A. arenosa*].
 - 11a. Basal leaves with terminal lobe larger than the 1–6 pairs of lateral lobes; seeds very narrowly winged or wingless *A. arenosa* subsp. *arenosa*
 - 11b. Basal leaves with terminal lobe subequal to or scarcely larger than the 4–9 pairs of lateral lobes; seeds conspicuously winged *A. arenosa* subsp. *borbasii*
 - 10b. Petals without lateral teeth on the claw; basal leaves lyrate-pinnatifid, lyrate, dentate, or entire [*A. lyrata*].
 - 12b. Basal leaves entire to toothed; older plants with an obvious, somewhat thickened, often branched caudex *A. lyrata* subsp. *petraea*
 - 12b. Basal leaves mostly lyrate to lyrate-pinnatifid; older plants with a fine, usually unbranched root crown.
 - 13a. Basal leaves usually pubescent and sparsely hirsute on petiole

- margins; petals 6–8 mm long; fruit to 1 mm wide; style 0.5–1 mm long *A. lyrata* subsp. *lyrata*
- 13b. Basal leaves glabrous to sparsely pubescent, petioles usually glabrous; petals (4–)5–6 mm long; fruit ca. 1.5 mm wide; style often less than 0.5 mm long *A. lyrata* subsp. *kamchatica*

Arabidopsis arenosa (L.) Lawalrée, Bull. Soc. Roy. Bot. Belg. 42: 242. 1969. Basionym: *Sisymbrium arenosum* L., Sp. Pl. 2: 658. 1753. TYPE: “In Germania, Helvetica” (holotype, LINN 836.22).

Subspecies *arenosa* is distributed in most of Europe (adventive in the north) and east to western Siberia. This is a highly variable taxon with a multitude of chromosomal races (Měsíček, 1970) that are sometimes segregated into weakly defined taxa, especially in the western Carpathians. The taxon approaches both *Arabidopsis suecica* and *A. neglecta* morphologically and is distinguished from these by the characters in the key above.

Arabidopsis arenosa (L.) Lawalrée subsp. **borbasii** (Zapałowicz) O’Kane & Al-Shehbaz, comb. nov. Basionym: *Arabis arenosa* (L.) Scopoli subsp. *borbasii* Zapałowicz, Rozpr. Wydz. Mat.-Przyr. Acad. Umiejeln., Dzial B, Nauki Biol. 52: 31. 1912. TYPE: Poland. Carpathians, Babia Góra monte, 1285–1725 m, Zapałowicz s.n. (lectotype, here designated, KRAM).

Subspecies *borbasii* is the only infraspecific taxon of *Arabidopsis arenosa* that can be consistently distinguished from subspecies *arenosa*. Like the latter, subspecies *borbasii* has variously been split into poorly defined races, and as recognized here, it is limited to central Europe.

Arabidopsis cebennensis (DC.) O’Kane & Al-Shehbaz, comb. nov. Basionym: *Arabis cebennensis* DC., Syst. Nat. 2: 234. 1821. TYPE: [France], “in locis asperis subumbrosis montium Cebennorum in horto Dei et Bramabiu” (holotype, G-DC).

This species is restricted to the mountains of southern France. Morphologically it is like *Arabidopsis pedemontana* except that it is larger in all respects and is sparsely pubescent rather than glabrous or subglabrous.

Arabidopsis croatica (Schott) O’Kane & Al-Shehbaz, comb. nov. Basionym: *Arabis croatica* Schott, in Schott, Nyman & Kotschy, Analect. Bot. 44. 1854. TYPE: Croatia, *F. Maly* s.n. (holotype, BP? not seen).

Endemic to Croatia. The species is morphologically and phylogenetically close to *Arabidopsis arenosa* and could conceivably be treated as a subspecies of that taxon.

Arabidopsis halleri (L.) O’Kane & Al-Shehbaz, comb. nov. Basionym: *Arabis halleri* L., Sp. Pl. ed. 2, 2: 929. 1763. TYPE: [Germany, Harzgebirge] as “Harcynia ad Clausthal, locis humidis” (holotype, LINN 842.11).

Subspecies *halleri* is distributed throughout Europe except in the western part, the far north, and most of Italy. It is a montane species that grows at elevations generally below timberline.

Arabidopsis halleri (L.) O’Kane & Al-Shehbaz subsp. **ovirensis** (Wulfen) O’Kane & Al-Shehbaz, comb. nov. Basionym: *Arabis ovirensis* Wulfen, in Jacquin, Collectanea 1: 196. 1786. TYPE: [Austria] Ovirensis supra Ebriacum in Valle Junonia percurrerem alpes, Wulfen s.n. (holotype, W).

Distributed in southern and eastern Europe, generally at high elevations above timberline, in the southeastern Alps, the Carpathians, and the northern Balkan Peninsula.

Arabidopsis halleri (L.) O’Kane & Al-Shehbaz subsp. **gemmifera** (Matsumura) O’Kane & Al-Shehbaz, comb. nov. Basionym: *Cardamine gemmifera* Matsumura, Bot. Mag. (Tokyo) 13: 49. 1899. TYPE: Japan. Prov. Shinano: monte Norikura, 1891, *K. Fuji* s.n. (holotype, TI).

A taxon of the Russian Far East, northeastern China, Korea, and Japan, typically occurring in shaded, moist situations from sea level onto low mountains.

Arabidopsis lyrata (L.) O’Kane & Al-Shehbaz, comb. nov. Basionym: *Arabis lyrata* L., Sp. Pl. 2: 665. 1753. TYPE: Canada, *D. Kalm* s.n. (holotype, LINN 842.8).

The species is circumboreal. Subspecies *lyrata* is entirely North American and ranges from Minnesota and Wisconsin south into Missouri, east into Georgia, north into Vermont, and west into Ontario. It is rare in Manitoba, Saskatchewan, Alberta, and

British Columbia (Mulligan, 1995). It is distinguished only with difficulty from the other subspecies of *Arabidopsis lyrata*, especially in areas where they come into contact. Mulligan (1995) treated the three subspecies of *A. lyrata* as distinct species, but as shown in the key above, the morphological differences between them do not support such a treatment.

***Arabidopsis lyrata* (L.) O'Kane & Al-Shehbaz subsp. *kamchatica* (Fischer ex DC.) O'Kane & Al-Shehbaz, comb. nov.** Basionym: *Arabis lyrata* L. var. *kamchatica* Fischer ex DC., Syst. Nat. 2: 231. 1821. TYPE: [Russia], Kamchatka, *Fisher s.n.* (holotype, LE).

Arabis morrisonensis Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30(1): 29. 1911. Syn. nov. TYPE: Taiwan, monte Morrison, 13,094 ft., Nov. 1905, *S. Nagasawa 680* (holotype, TI).

Arabis kawasakiana Makino, Bot. Mag. (Tokyo) 27: 24. 1913. Syn. nov. TYPE: Japan. Prov. Ise: Yokkaichi, *M. Kawasaki s.n.* (holotype, MAK).

Distributed in boreal regions of North America, far eastern Siberia, the Russian Far East, south to and including Korea and northern China, Japan, and south to Taiwan (collections in the last were described as *Arabis morrisonensis*). In the Russian Far East, subspecies *kamchatica* tends to grow closer to the sea than does subspecies *petraea*, which is a more continental taxon. Plants of subspecies *kamchatica* growing in sandy, ocean-side localities tend to have massive leaves and seem indistinguishable from those described as *Arabis kawasakiana* of Japan. In Japan, *Arabidopsis lyrata* subsp. *kamchatica* is found on more rocky, mountain slopes, and *Arabis kawasakiana* is found in sandy lowlands near the sea (Ohwi, 1965). Therefore, *Arabis kawasakiana* is treated as a synonym of *Arabidopsis lyrata* subsp. *kamchatica*, being just a large-leaved and less hairy ocean-side form. Mulligan (1995) treated subspecies *kamchatica* as a species of *Arabis*, whereas Rollins (1993) treated it as a variety of *Arabis lyrata*.

***Arabidopsis lyrata* (L.) O'Kane & Al-Shehbaz subsp. *petraea* (L.) O'Kane & Al-Shehbaz, comb. nov.** Basionym: *Cardamine petraea* L., Sp. Pl. 2: 654. 1753. TYPE: "In Angliae, Arvoniae, Mervinae, Sueciae, rupibus excelsis" (holotype, LINN 835.5).

Arabis media N. Busch, Bot. Mater. Gerb. Glav. Bot. Sada RSFSR 3(3-4): 11. 1922. Syn. nov. TYPE: [East Siberia]. "Zona arctica! et subarctica! ab ostio Lenae! usque ad Anadyr!, montes Sajanenses orientales!,

montes cis-et transbaicalenses! atque Jacutenses!" (holotype, LE not seen).

Distributed in parts of central, northern, and eastern Europe, east across boreal Asia to the Far East and boreal North America (Alaska and Yukon). Beginning in central Siberia, the taxon is increasingly similar to subspecies *kamchatica*, and many collections can only doubtfully be assigned to one or the other taxon. North American plants of subspecies *petraea* have been placed in *Arabis media* by Mulligan (1995).

***Arabidopsis neglecta* (Schultes) O'Kane & Al-Shehbaz, comb. nov.** Basionym: *Arabis neglecta* Schultes, Oestr. Fl. 2: 248. 1814. TYPE: Carpathians, *Schultes? s.n.* (holotype, M).

The species is endemic to high altitudes in the Carpathian Mountains (Czech Republic, Slovakia, Romania, Poland, and adjacent Ukraine).

***Arabidopsis pedemontana* (Boissier) O'Kane & Al-Shehbaz, comb. nov.** Basionym: *Arabis pedemontana* Boissier, Diagn. Pl. Orient. 1: 69. 1843. TYPE: [Switzerland], "In regione alpina montium Pedemontii, legi Aug. supra limitem arborum in collo inter Crissolo et Luzerna sitio" (holotype, G).

The species is restricted to northwestern Italy and, presumably extinct, in Switzerland. Morphologically similar to *A. cebennensis* except smaller (15–30 cm instead of 40–80 cm) and glabrous or subglabrous instead of sparsely pubescent.

***Arabidopsis suecica* (Fries) Norrlin, Meddel. Soc. Fauna Fl. Fenn. 2: 12. 1878.** Basionym: *Arabis suecica* Fries, Summa Veg. Scand. 1: 147. 1846. TYPE: Sweden. Prov. Södermanland: Strängnäs, *Fries s.n.* (lectotype, UPS; see Löve, 1961).

This species is shown to be an amphidiploid formed from *A. thaliana* and *A. arenosa* (O'Kane et al., 1997, and references therein) since the last glacial maximum. The species is distributed in Fennoscandia and the Baltic region and is probably adventive in a few locations in Germany. In addition to phylogenetic considerations, the fact that *A. suecica* is an ancient hybrid between *A. thaliana* and *Cardaminopsis arenosa* [*A. arenosa*] clearly supports the argument for combining *Cardaminopsis* with *Arabidopsis*.

***Arabidopsis thaliana* (L.) Heynhold, in Holl & Heynhold, Clav. Gen. Fl. Sachsen 1: 538.**

1842. Basionym: *Arabis thaliana* L., Sp. Pl. 2: 665. 1753. TYPE: "Europae septentrionalioris sabulosis" (holotype, LINN 842.5).

Arabidopsis thaliana is the conserved type of *Arabidopsis* (Greuter et al., 1994). Native to Eurasia, adventive elsewhere in the world, distributed in open or disturbed habitats in temperate regions.

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